COYOTE MOVEMENTS IN RELATION TO THE SPATIAL DISTRIBUTION OF SHEEP

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Abstract: Coyotes (*Canis latrans*) are a major predator of domestic sheep (*Ovis aries*) grazed on open range, but studies have not examined how coyote movement patterns change in relation to this temporally intermittent and spatially clumped food resource. Using 8 resident coyotes in the Sagehen Creek watershed, Nevada County, California, we found that coyote core areas (64% adaptive kernal estimator) overlapped more while sheep were in the basin, that at least 1 resident animal followed the sheep into other animals' core areas, and that coyotes did not avoid each other in areas where sheep were concentrated. We conclude that under the conditions of our study, territoriality in coyotes does not limit coyote access to sheep. Conclusions drawn by studies of coyotes not influenced by sheep may be spurious if inferences are made to sheep-influenced populations.

Previous studies of the movement patterns of coyotes examined their home range sizes (Gipson and Sealander 1972, Berg and Chesness 1978, Andelt and Gipson 1979, Woodruff and Keller 1982, Andelt 1985, Gese et al. 1988*a*) and their preference for habitats with high cover and high prey density (Litvaitis and Shaw 1980, Andelt and Andelt 1981). Studies that examined the spatial distribution of coyotes around areas with a concentrated food supply produced conflicting results. On a turkey production site, coyote families either used exclusively or partitioned the use of the site (Althoff and Gipson 1981). However, all home ranges overlapped with no evidence of territoriality among 13 coyotes near a cattle feedyard (Danner and Smith 1980). Coyote territories were significantly larger during a period of prey scarcity in 1 study area (Mills and Knowlton 1991). Coyote group size increased with the volume of large prey in the diet (Gese et al. 1988*b*), and home range size was shown to vary directly with coyote group size (Bowen 1982). Prey availability appears to have an effect on coyote space use.

Future studies should examine coyote space use in the home range (Laundré and Keller 1984).

Small regions of concentrated use in home ranges are core areas (Springer 1982). Probably, core areas are primarily used for hunting and resting and peripheral areas are primarily used for ranging behaviors (Laundré and Keller 1981). Core areas can be considered to be equivalent to territories (Mills and Knowlton 1991).

Although coyotes are a major predator of domestic sheep (Connolly et al. 1976, Timm and Connolly 1977, Connolly 1982), the effects of this prey resource on coyote spatial distribution has not been thoroughly examined. Also, there is little information of coyotes in mountainous areas of the western United States where many summer sheep permits are located. Evaluating methods of controlling coyote predation on sheep requires understanding coyote behavior in relation to the spatial distribution of sheep.

To investigate the influence of sheep on a coyote population, we examined 3 hypotheses:

Hypothesis 1 (H1): Territoriality prevents overlap of coyote core areas in places where sheep are grazed, therefore the amount of core area overlap will not change in relation to the presence of sheep.

Hypothesis 2 (H2): Territoriality prevents coyotes from following moving sheep and trespassing into core areas of other coyotes.

Hypothesis 3 (H3): If coyote core areas over-

lap in places where sheep are grazed, they will avoid each other to temporally partition the resource.

STUDY AREA

We worked in a 105 km² watershed about 13 km north of Truckee, California in the Tahoe National Forest. Elevation in the nearby areas ranged from 1,880 to 2,620 m. The area was characterized by long, cold winters and warm, dry summers with nightly temperatures falling below 0 C, often at all times of year. Most of the annual precipitation (91 cm) fell as snow during winter. Forested areas were dominated by Jeffrey pine (*Pinus jeffreyi*) and white fir (*Abies concolor*). Brush fields contained deerbrush (*Ceanothus velutinus*) and greenleaf manzanita (*Arctostaphylos patula*). Sagebrush (*Artemisia tridentata*) dominated on lower, dry slopes. Small stands of lodgepole pine (*Pinus contorta* var. *murryana*) and aspen (*Populus tremuloides*) occurred near springs, meadows and streams. Red fir (*Abies magnifica*), mountain hemlock (*Tsuga mertensiana*) and western white pine (*Pinus monticola*) dominated at higher elevations (Morrison et al. 1985).

Sagehen Creek runs through a central valley and into Stampede Reservoir, resulting in topographical and hydrological variations in the study area. Areas of different-aged vegetation occurred as a result of fires in 1926, 1960 and 1968. Domestic animals used areas with varying intensity; 200–500+ ewes, usually with lambs, were grazed through the basin during the summer.

METHODS

Capture and Restraint

Coyotes were trapped using steel leghold traps with offset, padded jaws and short anchor chains to reduce injury and stress (Hawthorne 1970, Olsen et al. 1986). We trapped in 3 periods during June-July and September-October of 1993 and June of 1994. We increased pan tension by tightening the tension-screws on the pan hinges to minimize capture of small non-target species. Daily visual checks of the trap sites were made to reduce time in trap and chances of injury. Trapped coyotes were immobilized with a pin-stick and then bound with vet-wrap or electrical tape, processed, and released on-site.

Telemetry

We used 5 5-element Yagi-antenna null-peak telemetry stations installed around the study area to reduce error from the long distances between receivers and transmitters (White 1985, White and Garrott 1986, White and Garrott 1990). Telemetry station positions were determined by locating them with Global Positioning System (GPS) equipment (Trimbel Navigation, standard deviation of all locations <4.1 m).

Three observers, working at 3 stations, attempted to locate simultaneously each animal once hourly during 8 4-hour tracking sessions per week. Tracking sessions were sunrise (2 hr before to 2 hr after sunrise), sunset (2 hr before to 2 hr after sunset), day (4 hr equally spaced between sunrise and sunset), and night (4 hr equally spaced between sunset and sunrise). Coyote locations were recorded as Universal Transverse Mercator Grid System coordinates by using the program LOCATE II (Truro, Nova Scotia, Canada).

We estimated system error by calculating the distance between test collars and their estimated location. We placed test collars throughout the study area at sites readily located on a 1:24,000 USGS map (e.g., road intersections and creek confluences). We used 7 collars that were thought to be live coyotes by the trackers to minimize the bias resulting from non-double-blind tests of telemetry systems (Mills and Knowlton 1989) and 24 single-blind locations. Median error was 341 m.

Seasons

We divided data into 4 seasons for analysis. Seasons, based on coyote biological seasons (Smith
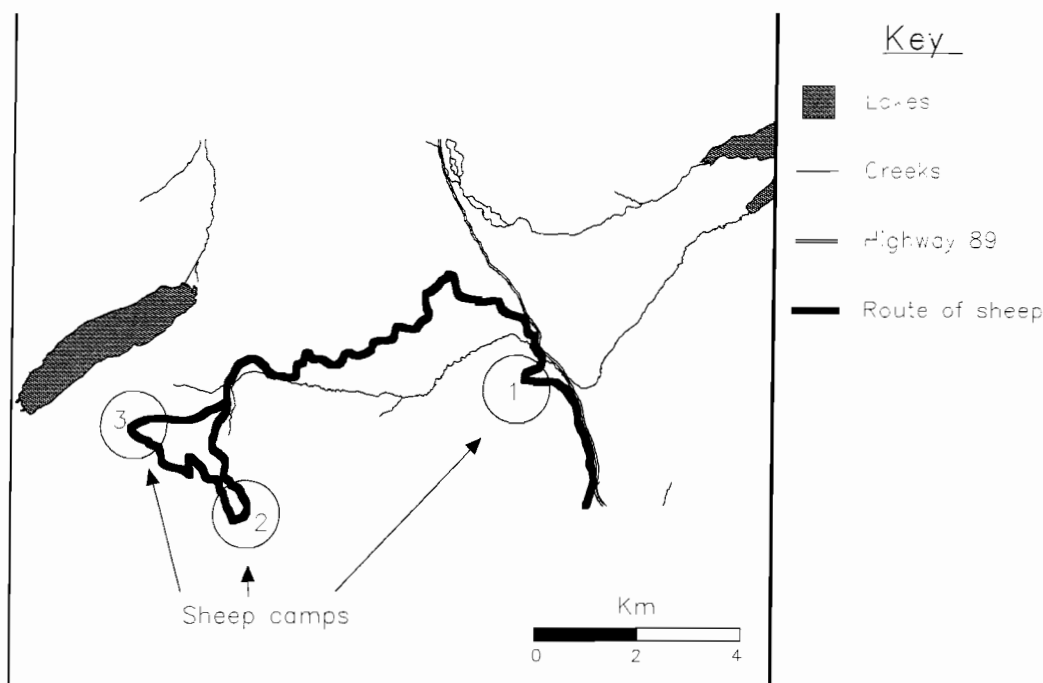
Fig. 1.   Approximate route of domestic sheep through the Sagehen Creek, California study area. Sheep entered camp 1 on 6 July 1994, moved to camp 2 on 12 July, moved to camp 3 on 16 July and stayed until 25 July. They returned to camp 1 where they stayed until they left the study area on 30 July.

et al. 1981, Laundré and Keller 1984), were: (1) Breeding (1 Jan-15 Mar), (2) Pre-pup (16 Mar-30 Apr), (3) Pup rearing (1 May-31 Jul), and (4) Dispersal (1 Aug-31 Dec). Data collection was from 1 August 1993 to 31 July 1994.

Sheep

About 600 ewes and 500 lambs were herded through the study area during the 1994 pup rearing season (Fig. 1). Sheep were grazed in 3 camps for about 1 week at a time and then moved to the next camp. Because sheep were always kept together, 1 ewe was radiocollared and her location indicated the location of the entire band. The sheep camp boundaries were based on day and night locations of the sheep. A human herder and his dogs remained with the sheep while the band was in the study area; he attempted to determine the cause of death of depredated sheep.

Home Ranges

We calculated home ranges with the program CALHOME using the adaptive kernal method (John Kie, Pac. Southwest For. and Range Exp.

Station, Fresno, Calif.). This method is less susceptible to the effects of outliers and the inclusion of non-used areas in the home range than the minimum convex polygon method (Mohr 1947, Odum and Kuenzler 1955, Jennrich and Turner 1969). Worton (1987:295) promoted the use of this method because the "kernal methods provide a very good means of highlighting areas of concentrated activity."

We partitioned home ranges into core and inter-core areas using animal location probability contours. Core areas indicated areas of high animal use. To identify "that area traversed by the individual in its normal activities" (Burt 1943) and not an area that also included an animal's occasional forays outside of it, the size of the area within each probability contour was graphed against the different probability levels. As this graph neared a vertical trajectory, each larger probability contour became more sensitive to outlying locations and thus did not aid in appropriately defining the animal's home range. Therefore, a home range was defined as that area within the probability contour beyond which most coyote's graphs became nearly ver-
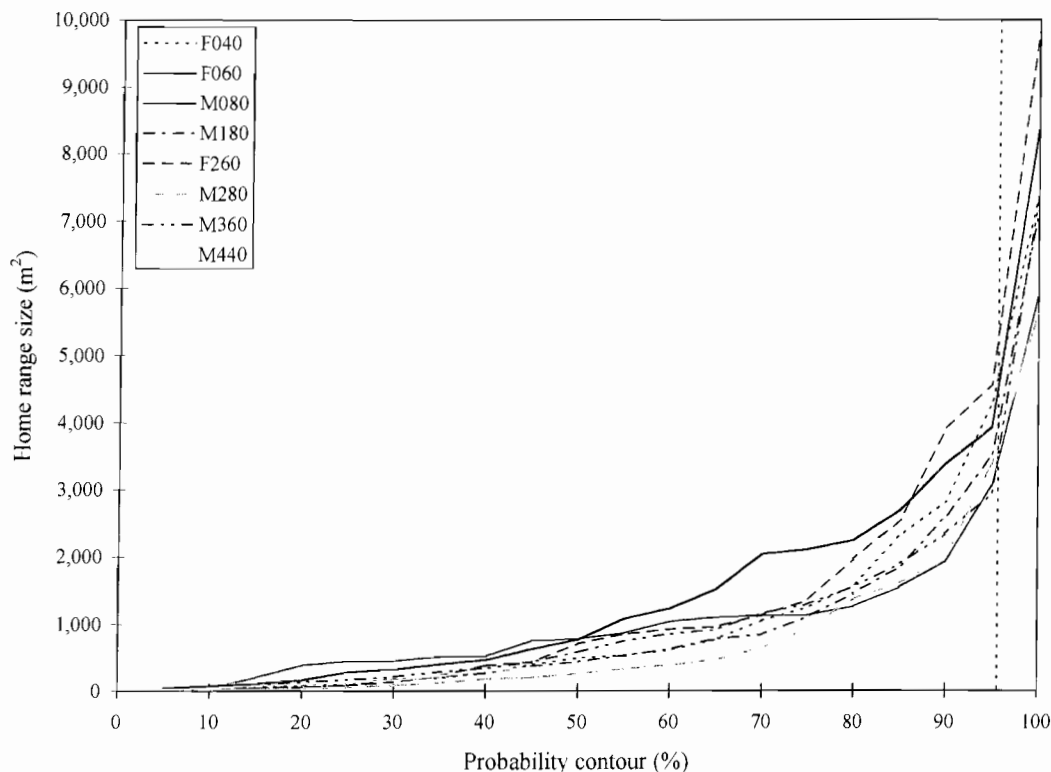
Fig. 2.   Home range size-probability contour graphs for 8 coyotes at Sagehen Creek, California during 1993–94. Probability contours were calculated with program CALHOME's adaptive kernal method. The area within the 96% contour defined a coyote home range.

tical. This occurred at the 96% probability contour (Fig. 2). The core area was arbitrarily defined as the probability contour that was two-thirds of the total (i.e., 64%). The two-thirds value was chosen because it can be thought of as being close to the actual distribution of points falling within 1 standard deviation of the center of the home range (Macdonald et al. 1980). The adequacy of sample sizes for seasonal home ranges was evaluated using area/observation curves (Odum and Kuenzler 1955).

Autocorrelated points can influence the calculation of home range size (Swihart and Slade 1985a,b). The sampling scheme for this study resulted in autocorrelated points (Solow 1989). We did not attempt to locate and discard autocorrelated coyote locations because our analyses were not based on coyote home range sizes. Furthermore, because the sampling scheme remained constant throughout the study, any bias introduced in calculating the boundaries of home ranges would have been controlled by the analyses that we performed.

Hypotheses

H1.—Overlap of adjacent and non-affiliated coyote core areas was examined by first measuring the amount of core area overlap (in km²) during each biological season. Two coyotes were considered to have adjacent territories if their core areas were next to each other. That is, there was no space for, or evidence of, other collared or non-collared coyote home ranges separating them. The amount of overlap between members of a social group (e.g., mated pairs who had nearly complete overlap) was excluded from the analysis. An ANOVA was used to detect differences in mean core area overlap between seasons. To improve the normality of residuals and to stabilize variances, the amount of overlap was first transformed by adding 1, squaring the value and then dividing it into -1 (Kirby 1993) before submitting it to ANOVA procedures.

H2.—To determine if coyotes followed sheep in a measurable fashion, we compared simultaneous distances between coyotes and sheep to
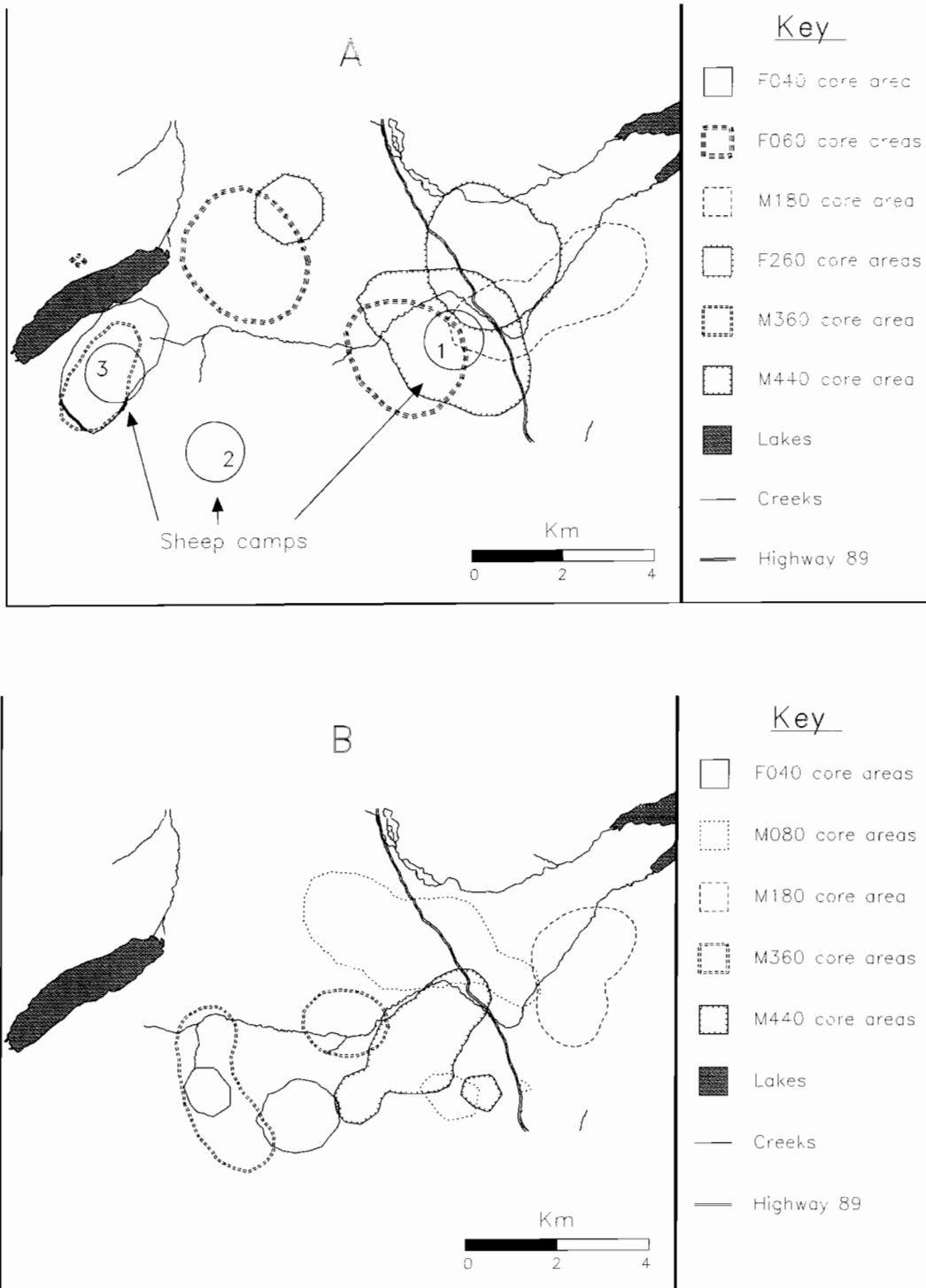
Fig. 3. Coyote core areas, A, during season 3 (pup-rearing, 1 May–31 Jul 1994) including sheep camps and, B, season 4 (dispersal, 1 Aug-31 Dec 1993) at Sagehen Creek, California.

expected distances as estimated by randomly pairing all pup-rearing season locations 500 times (with replacement). We chose 500 m as the distance at which coyotes were considered to be close because distances less than this are probably biologically relevant (i.e., 2 coyotes are likely to become aware of each other at some distance less than, but not >500 m), and because it was wide enough to allow for telemetry error. If coyotes were close to the sheep more often than expected using a Yate's-corrected Chisquare test (Zar 1984), we concluded that they followed the sheep, and if they were close to the sheep less often than expected, we concluded that they avoided them (Sargeant et al. 1987, Doncaster 1990).

H3.—To identify whether 2 coyotes showed a simultaneous aversion to a sheep-use area (and thus temporally partitioned its use), we regressed the simultaneous (within 20 min) distances of those 2 coyotes to the midpoint of that sheep use area. The simultaneous distance analysis was only performed for coyotes that exhibited core area overlap in the area of sheep camps.

RESULTS

Of the 16 coyotes captured during the course of the study, 8 (5 M, 3 F) were used for analysis because they maintained stable home ranges in the study area and were located enough times to allow home ranges to be calculated. These 8 animals were located 1,291 times with a mean number of 64 (range 20–207) locations/season/individual. The calculated core area size was not related to the sample size (regression of core area size vs. square root of sample size: $P = 0.80$, power $= 0.81$, Zar 1984), nor could we conclude that core area size was related to season (ANOVA: $P = 0.74$, power < 0.30, Zar 1984). There were no confirmed kills of sheep by coyotes, but 4 sheep were missing when the sheep left the study area.

Hypotheses

H1.—Mean core area overlap varied among seasons ($P = 0.038$). Mean overlap was greatest during season 3, while sheep were in the study area (0.914 km^2, $n = 10$)(Fig. 3), and less during seasons 4 (0.118 km^2, $n = 7$), 1 (0.063 km^2, $n = 7$), and 2 (0.0 km^2, $n = 5$) when sheep were absent.

H2.—Six coyotes were located simultaneously with the sheep enough times to allow analysis
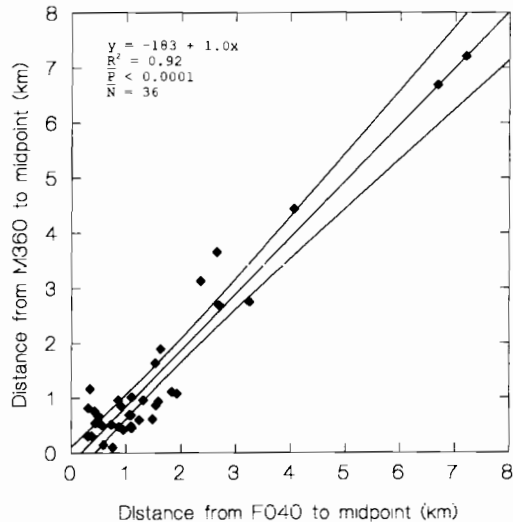

Fig. 4. Graph of the simultaneous distances of the coyote pair F040 and M360 to the midpoint of the sheep camp that was located in their 1994 pup-rearing season core area at Sagehen Creek, California. Curved lines represent the 95% confidence intervals around the regression.

of correlated movement behaviors while the sheep were in the basin. Five animals showed no evidence of following or avoiding the sheep, but 1 coyote, an adult male, followed the band ($P = 0.004$). His normal home range enclosed sheep camp 1, but he also made a foray into the core area of an adjacent mated pair, whose core area encompassed sheep camp 3 (Fig. 3) when the sheep were in it.

H3.—The midpoint of sheep camp 1 for season 3 was an area of high overlap by 4 coyotes (Fig 3). However, these coyotes showed no simultaneous attraction to or avoidance of this area. The mated pair whose overlapping home ranges encompassed sheep camp 3 showed a strong simultaneous attraction to the center of this area ($P < 0.0001$) (Fig. 4).

DISCUSSION

Although coyotes actively scent mark (Barrette and Messier 1980) and otherwise exhibit territoriality (Bekoff and Wells 1980, Wells and Bekoff 1981, Windberg and Knowlton 1988) they may relax this behavior when intermittent and localized food sources are predominant (e.g., carrion in winter, Camenzind 1978, Bekoff and Wells 1980, E. M. Gese, Univ. Wis., pers. commun.). The high degree of overlap of coyote

home ranges at sheep camp 1 (Fig. 3) suggests that coyote territoriality may not effectively prevent all coyotes from having access to a herd of sheep. At least 2 of the 3 collared females whelped during season 3. Coyote F040's core area did not overlap with any other coyote's except her mate's, but F060, who also whelped, maintained a core area that overlapped those of 3 other coyotes, although they did not appear to be socially affiliated.

Woodruff and Keller (1982) captured most coyotes near the edge or outside of their territories, and Windberg and Knowlton (1990) reported that although individual coyotes were less vulnerable to traps in the interiors of their home ranges, the number of coyote captures did not differ based on trap location. Coyotes may exhibit the use of an "area occupied more or less exclusively by an animal or group and defended by overt aggression or advertisement" (Drickamer and Vessey 1986:350), i.e., coyotes establish territories. However, trespassing (as documented in this study) may be relatively common as indicated by previous studies. Sheep, or possibly the effects of their presence (e.g., increased small mammal vulnerability due to decreased vegetative cover) attracted at least 1 coyote to move with them into an adjacent mated pairs' core area. Therefore, coyote territoriality (as evidenced by minimally and non-overlapping core areas during other seasons) does not wholly prevent coyotes from following sheep through neighboring territories.

Coyotes did not appear to partition their simultaneous use of sheep camp 1, but could have been congregating as did coyotes in Jackson Hole, Wyoming (Camenzind 1978). The simultaneous attraction of the mated pair to the center of sheep camp 3 was due to their strong social bond; these 2 coyotes usually traveled together. This type of behavior was reported by Andelt et al. (1979) for mated pairs. Their den site (with pups) was located less than 1 km from sheep camp 3.

Although territoriality has been demonstrated in coyotes, discrepancies such as those reported by Danner and Smith (1980) may be explained partly by a breakdown of territoriality in areas of high food resources, similar to behaviors of normally solitary bears (*Ursus arctos*) around garbage dumps and salmon streams (Craighead and Mitchell 1982). We did not attempt to unequivocally demonstrate territoriality in this study, but believe that it exists in

some form for Sagehen coyotes, as evidenced by low core area overlap in seasons 1 and 4, and no overlap during season 2.

We detected core area overlap in areas that sheep were using, sheep-following behavior by 1 coyote that included core-area intrusions and no apparent temporal partitioning of sheep-use areas, and therefore we rejected all of our initial hypotheses. The question of whether or not all coyotes kill sheep may be of little relevance, since a depredating coyote may gain access and kill sheep in other coyotes' core areas. At Sagehen, numerous coyotes had access to sheep even though they were in the core areas of other animals, so management that selectively leaves territorial non-sheep-killing coyotes in a population would not necessarily safeguard against sheep kills by other coyotes. Using management techniques such as denning or chemosterilization to decrease coyote reliance on sheep for provisioning pups (Till and Knowlton 1983) and selective removal of known coyote sheep-killers may reduce the overall proportion of sheep-killing coyotes in a population. However, beneficial secondary effects of leaving territorial, non-sheep-killing coyotes within a population may be negligible because they do not necessarily prevent access to sheep by other coyotes. Further research should quantify the amount of trespassing by coyotes that occurs.

We did not simultaneously monitor a control population of coyotes and cannot conclude a cause and effect relation between sheep movements and coyote movements. Indirect effects of sheep presence, or the habitats where sheep are typically grazed, may have influenced coyote movements. These confounding factors may have been important in this study because no confirmed coyote kills were documented. However, in regard to coyote control and management, the conclusion remains: Coyote movements appear to be influenced in areas where sheep are grazed.

Because the spatial distribution of sheep, or effects related to their presence, can influence coyote movements, it is important to incorporate sheep effects into future research and management programs. Conclusions drawn by studies of coyotes not influenced by sheep may become spurious if inferences are made to sheep-influenced populations. Further research should identify the distance within which coyotes are influenced by roaming bands of sheep to delimit a coyote population that may require control.

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